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# FILTERING RATES OF THE HARD CLAM (*VENUS MERCENARIA*) DETERMINED WITH RADIOACTIVE PHYTOPLANKTON

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## ABSTRACT

Filtering rates of the hard clam, *Venus mercenaria* L., were determined by ascertaining the number of radioactive phytoplankton removed from water pumped through the filtering mechanism of the clam. If the cells are not completely filtered from the water pumped, the filtering rate of the clam is less than the pumping rate. The term "filtering rate" refers to the volume of water from which the cells are removed per unit of time.

The labeling of algae with radioactive phosphorus made it possible to follow smaller initial populations than have been used in most previous investigations, yet it provided a means of accurately measuring slight changes in these populations. The number of cells present at the beginning of an experiment and the size of these cells influenced the filtering rate. The filtering rate in unialgal suspensions was different from that in mixed suspensions. The filtering rate in natural populations of phytoplankton was higher than in unialgal suspensions of green algae and lower than in unialgal suspensions of diatoms.

Silt had an adverse effect on the hard clam, since it reduced the filtering rate and stimulated the formation of pseudofeces. A similar effect was produced by the presence of *Chlorella* in the water. In relating filtering rates to size of clams, more water per gram of meat was filtered by small clams than by large clams.


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# FILTERING RATES OF THE HARD CLAM (*VENUS MERCENARIA*) DETERMINED WITH RADIOACTIVE PHYTOPLANKTON

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Among the more-important factors affecting the efficiency of the filtering mechanism of filter-feeding animals are size and number of particles present in the water. Problems relating to nutrition may be more easily solved when the factors controlling the rate at which water is filtered and the efficiency of removal of food particles have been determined. Using either a direct or an indirect method, many measurements have been made of the rate at which water is transported through the filtering mechanism of lamellibranchs. In the direct method, the water pumped is separated and measured (Galtsoff, 1926, 1928; Nelson, 1935, 1936; Loosanoff and Engle, 1947; and Collier, Ray, Magnitzky, and Bell, 1953). Water pumped through the gills may or may not be filtered; only if the particles are removed from the water pumped can it be considered to have been filtered. In some investigations both the amount of water pumped and the efficiency of the filtering mechanism in removing particles from the water have been determined simultaneously. From the rate of removal of particles the volume of water filtered can also be determined.

With many lamellibranchs a direct measurement of the pumping rate is not practicable. As a result, indirect methods based on the rate of removal of particles from the water by the filter-feeding mechanism of the animal have been developed. The volume of water pumped can be calculated only if the filtering mechanism removes all the suspended particles from the water passing through it. If any cells escape, the filtering rate will naturally be less than the pumping rate. For this reason only the volume of water from which the cells are removed per unit of time will be referred to as the filtering rate. It is incorrect to use the terms "filtering rate" and "pumping rate" interchangeably, even though this has occurred in the literature.

In most investigations with lamellibranchs, the removal of particles by the filtering mechanism has been followed with chemical determinations and photometric techniques. Calcium carbonate, colloidal graphite, and unicellular algae were used as particles in experiments measuring the volume of water filtered by lamellibranchs (Fox, Sverdrup, and Cunningham, 1937; Jørgensen, 1943, 1949; Rao 1953; and Ballantine and Morton, 1956). Also, a neutral red solution has been employed in comparing the amount of water pumped under different environmental conditions (Cole and Hepper, 1954). Another method for determining filtering rates has been the use of radioactive phosphorus with a colonial diatom (Jørgensen and Goldberg, 1953). The labeling of unicellular algae, that is, the incorporation of radioactive phosphorus into the protoplasm for use in filter-feeding experiments, has been investigated in detail by Rice (1953). This has made possible a much more sensitive and accurate technique for determining small changes in the number of cells in a volume of water. Filtration rates based on the reduction in numbers of unicellular algae using radioactive-labeled cells were determined by Chipman and Hopkins (1954).

In a review of the literature no reference was found to the filtering rates of the hard clam, *Venus mercenaria* L. Thus, the purpose of this investigation was to determine and compare the filtering rates of this clam relative to (1) the number of algal cells present at the beginning of the experiments, (2) size of the cells used, (3) removal of a species in unialgal and in mixed suspension, (4) removal of cells in unialgal suspension and in natural populations, and (5) removal of cells in unialgal suspension before and after adding silt.

Note—Approved for publication, March 18, 1957. Fishery Bulletin 129.

## MATERIALS AND METHODS

Four species of planktonic algae were fed to hard clams in both single and mixed cultures. The algae used and their sizes were as follows:

| Species: | |
|---|---|
| Chlorophyceae: | *Size:* |
| *Nannochloris atomus* | 2$\mu$ (in diameter) |
| *Chlorella* | 4$\mu$ (in diameter) |
| Bacillariaceae: | |
| *Nitzschia* sp | 19$\mu$ x 5$\mu$ (length and width) |
| *Nitzschia closterium* | 43$\mu$ x 4$\mu$ (length and width) |

Cells used in feeding experiments were first grown in sea-water culture medium to which no phosphorus was added (Rice 1953). Carrier-free radioactive phosphorus ($P^{32}$) placed in these cultures was rapidly taken up by the cells. All algal cells used in experiments were taken from cultures only a few days old, so that they were in a state of rapid division. Prior to starting an experiment, a portion of medium was filtered and the $P^{32}$ in the cells was measured. Also, the number of cells in the culture was determined by cell counts made with an improved Neubauer haemocytometer. After determining the radioactivity contained in the cells and the number of cells in the culture, it was possible to dilute the proper portion of culture with enough sea water to give the desired population of cells for the feeding experiment.

Any subsequent measurement of radioactivity contained in cells from a portion of the suspension could be converted to represent the number of cells present at that particular time. By incorporating sufficient amounts of $P^{32}$ in the cells, a small reduction in the number of cells in suspension in the water with the clam could be followed accurately. This was possible even when the population size was considerably smaller than that occurring in nature.

The clams used in this investigation were collected in the Beaufort area and kept in the laboratory in running sea water when they were not being used in experiments. They ranged from 58.6 mm. to 88.6 mm. in length and from 45.1 to 73.6 mm. in height, with the exception of smaller clams used in experiments to determine the volume of water filtered on the basis of weight of the clams. A total of 150 experiments were conducted over a period of 1 year. In each experiment, a clam was placed in a battery jar containing 2 liters of freshly collected and filtered sea water with a salinity of 30 to 35‰ and a temperature of 23°±2° C. A stirrer was used in all experiments to rapidly mix the filtered water with the nonfiltered and to prevent the cells from settling. Controls, consisting of the same number of cells suspended in an equal volume of water in which no clam was placed, showed that the stirring was sufficient to prevent the cells from settling.

Samples of the suspension of 10 cc. each were removed with a pipette from the same location in the battery jar before placing the clams in the containers and at 15-minute intervals after the clams had opened. To remove the cells from the water, each sample was filtered through a millipore filter. The filter was placed in a metal planchet and the amount of radioactivity in the cells was measured.

If the clam filters all the cells from the water that passes through the gills, it is possible to calculate the rate of water pumped by the application of Jørgensen's formula (1943):

$$m=\frac{(\log conc_o-\log conc_t)\cdot M}{\log e\cdot t}$$

In this formula, $m$ is the quantity of water pumped in liters per hour, $M$ is the volume of cell suspension in liters, and $conc_o$ and $conc_t$ are the cell concentrations at the initial time and after $t$ hours of time. It is very possible that some cells pass through the gills without being removed from the water. Thus, the volume of water calculated by this formula will be referred to as the filtering rate, which no doubt is lower than the actual pumping rate.

## RESULTS

To determine a representative filtering rate for the clam, it is necessary to know whether the efficiency of the gills in retaining particles is always the same in a given animal. Otherwise, it is not possible to ascertain whether a variation in the filtering rate is the result of a change in filtering efficiency or in the volume of water pumped. The animal, no doubt, changes the rate at which water is pumped through the mantle cavity. In addition to the formation of mucus on the gill surface, the animal can also change the size of the gill pores making it very unlikely that the efficiency of removal of particles is constant.

A comparison was made of variations in filtering ates obtained at different times for an individual lam in suspensions of one species of algae. Exper- ments with clam F, which covered a 2½-month nterval of time and population sizes of *Nanno- hloris* ranging from 74 million to 2,236 million ells per liter, are shown in table 1. The highest nd lowest filtering rates were based on the re- noval of cells during a 15-minute interval of time, vhile the average filtering rate was based on eight 5-minute intervals. The highest filtering rate bserved was about 4 liters per hour and the lowest vas 0.1 liter per hour. The average filtering rates anged from 0.8 to 2.1 liters per hour. Experiments onducted on two different days with 161 million ells per liter gave average filtering rates of 1.6 nd 1.7 liters per hour. There appears to be no elation between the numbers of cells used in these xperiments and the average filtering rates ob- ained. The experiment with 153 million cells per liter gave the largest average filtering rate, vhile the experiment in which 161 million and ,236 million cells per liter were used gave about he same filtering rates.

The growth of clam F during the interval of ime tested in these experiments was probably of io significance in influencing the filtering rates btained; however, the filtering rate per gram of neat for clams of different weights was investi- ated. In table 2 it can be seen that the rate of iltering per gram of meat decreases as the size of he clam increases.

To compare the rates obtained when clams are iltering particles of different sizes, experiments vere conducted with clams using suspensions of our species of planktonic algae (table 3). The ighest and lowest filtering rates were based on the emoval of cells during a 15-minute interval of time, while the average filtering rate was based on eight 15-minute intervals. The highest, lowest, and average filtering rates of the clams were consistently higher in suspensions of diatoms than of green algae.

In figure 1 are typical curves for each of the four species of algae, showing the decrease in numbers of cells due to the filtering activity of the clam. The slopes of the curves showing the removal of the two small green forms are not as steep as are those of the diatoms. The rates of removal for the two green algae were similar; also, the rates of removal of the two species of diatoms were in close agreement. It is of interest that the rates of removal of the green algae formed straight lines, while those of the diatoms gave sigmoid curves, when plotted on semilog graph paper. Even though the number of cells present in suspension was the same for the diatoms as for the green algae, the diatoms represented a larger amount of protoplasm.

A comparison was then made of the decrease in number of cells filtered when both large and small initial populations of *Nannochloris* were used (fig. 2). Regression lines were calculated and have been drawn through the points. It can

TABLE 1.—*Filtering rates of clam F in* Nannochloris *suspensions of various concentrations at different times*

[Concentration: cells/liter × $10^6$]

| Date | Concentration | Filtering rates (liter/hour) | | |
|---|---|---|---|---|
| | | Highest | Lowest | Average |
| Nov. 17, 1955 | 768 | 1.8 | 0.3 | 1.0 |
| Nov. 19, 1955 | 153 | 4.2 | .3 | 2.1 |
| Nov. 30, 1955 | 656 | 2.3 | .1 | 1.0 |
| Dec. 12, 1955 | 775 | 2.3 | .4 | .8 |
| Dec. 13, 1955 | 161 | 2.5 | .9 | 1.6 |
| Dec. 14, 1955 | 161 | 2.7 | .9 | 1.7 |
| Jan. 17, 1956 | 74 | 1.4 | .4 | 1.0 |
| Jan. 20, 1956 | 83 | 1.9 | 1.0 | 1.1 |
| Jan. 27, 1956 | 2,125 | 2.2 | .4 | 1.0 |
| Feb. 1, 1956 | 2,236 | 2.1 | 1.1 | 1.6 |

TABLE 2.—*Filtering rates per gram of meat for hard clams of different weights in* Nannochloris *suspension*

| Number of experiments | Wet weight of meats (gm.) | Filtering rate (l./hr./gm.) |
|---|---|---|
| 5 | 6.2 | 0.15 |
| 5 | 10.9 | .10 |
| 10 | 20.9 | .07 |
| 10 | 28.0 | .05 |

TABLE 3.—*Filtering rates of hard clams based on removal of four different species of algae in suspension*

[Concentration: 74 × $10^6$ cells per liter]

| Species | Filtering rates (liter/hour) | | |
|---|---|---|---|
| | Highest | Lowest | Average |
| Clam F: | | | |
| *Nannochloris* | 1.4 | 0.9 | 1.0 |
| *Chlorella* | 3.7 | .5 | 1.8 |
| *Nitzschia* sp. | 6.9 | .9 | 3.5 |
| *Nitzschia closterium* | 6.1 | 1.3 | 3.9 |
| Clam R: | | | |
| *Nannochloris* | 1.9 | .7 | 1.3 |
| *Chlorella* | 1.0 | .1 | .6 |
| *Nitzschia* sp. | 4.8 | 1.7 | 3.1 |
| *Nitzschia closterium* | 5.0 | 1.6 | 3.5 |
| Clam S: | | | |
| *Nannochloris* | 4.2 | 1.0 | 2.2 |
| *Chlorella* | 1.9 | .6 | 1.3 |
| *Nitzschia* sp. | 6.8 | 1.8 | 4.2 |
| *Nitzschia closterium* | 7.0 | 2.8 | 4.7 |

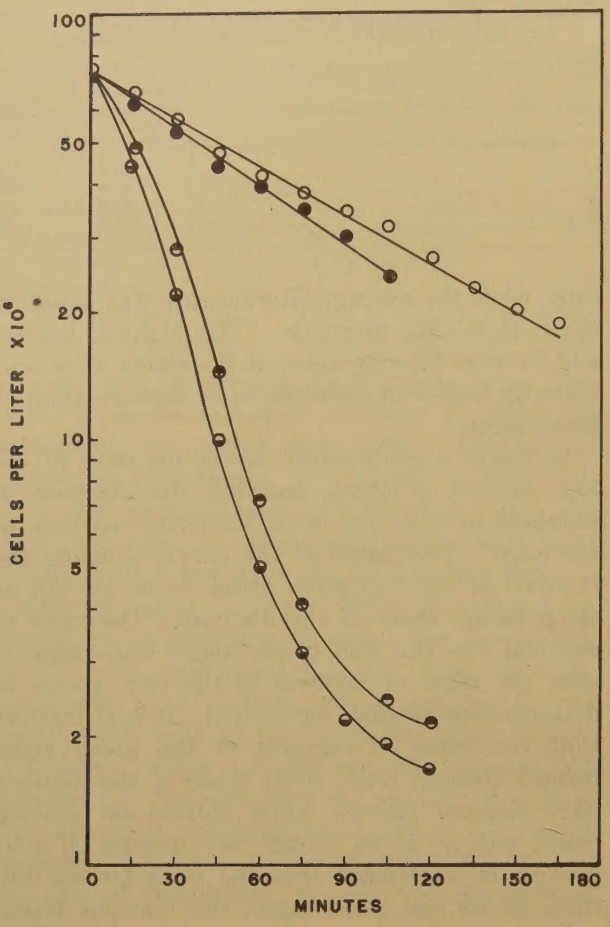



FIGURE 1.—Rates of removal of unicellular phytoplankton from suspension by the filter-feeding activity of the hard clam. (○ = *Nannochloris;* ● = *Chlorella*; ◓ = *Nitzschia* sp.; and ◒ = *Nitzschia closterium.*)

be seen that the slopes of these two lines are about the same. From this comparison it can be concluded that the filtering rate is independent of the number of cells used in these experiments.

It is also of interest to compare the effect of numbers of diatoms in suspension upon the filtering rate of the hard clam, as shown in figure 3. There is much similarity between the curves representing the removal of cells at the two intermediate population sizes. The curves representing the highest and the lowest population sizes, while being somewhat similar, are quite different from the curves for the intermediate-size populations. Obviously, the number of *Nitzschia closterium* cells in the water does affect the rate at which the clam removes these diatoms.

The rate of removal of a given species of algae by the clam differs in unialgal suspensions from that in mixed algal suspensions (fig. 4). The rate of removal of *Nitzschia closterium* cells is more rapid when this diatom is alone in a concentration of 5 million cells per liter than when 5 million *Chlorella* cells per liter are also present. The rate of removal of 74 million *Nannochloris* cells per liter, however, was more rapid when 70 million *Nitzschia closterium* cells per liter were also present than when the *Nannochloris* cells were used alone.

In many instances, data collected in the laboratory do not give a reliable index of conditions in nature. Thus, an effort was made to determine the rate of removal of particles by the clam from a natural population for comparison with data collected on unialgal suspensions in the laboratory. This is a difficult task which has not been attempted very many times and probably could not have been undertaken here without the use of radioisotopes.

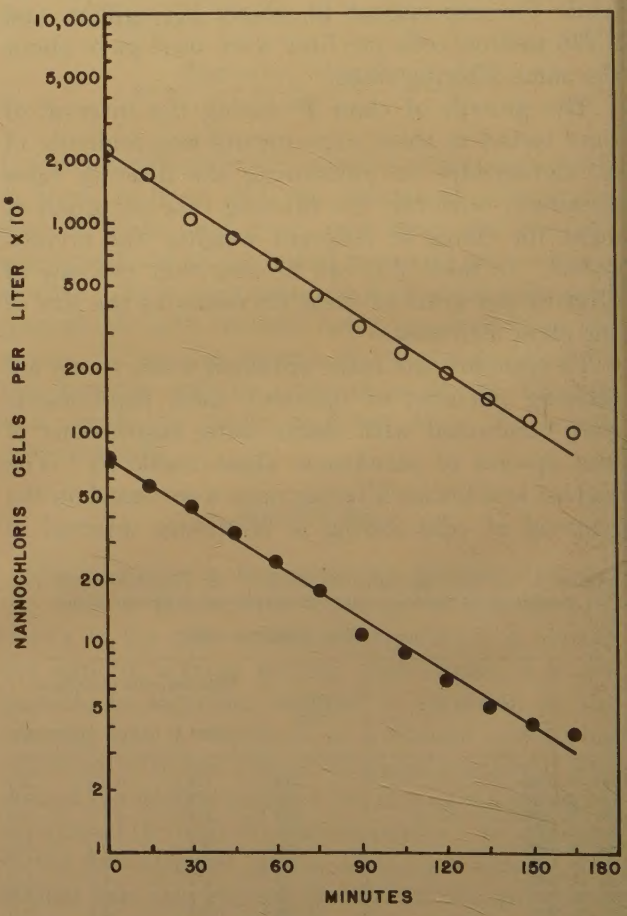
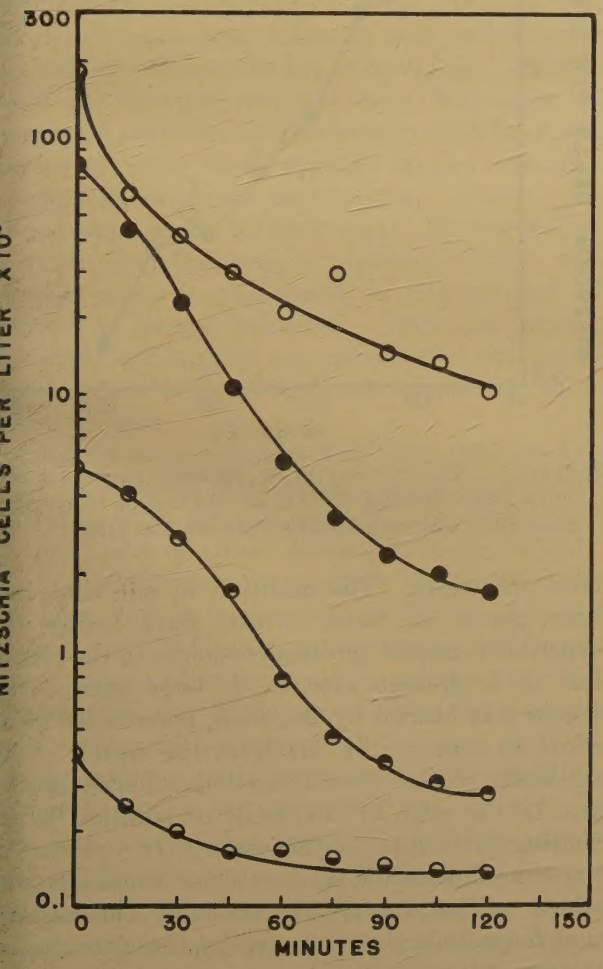



FIGURE 2.—Rates of removal by the hard clam of *Nannochloris* at two different population sizes.

From previous experiments conducted in our laboratory we knew that dividing cells take up much more radioactive phosphorus than nondividing cells. Also, it was found that the adsorption of $P^{32}$ on the surface of the cells was small in comparison with that taken up due to metabolic activity. From this information it is probably correct to assume that the disappearance of $P^{32}$ from solution when added to freshly collected sea water placed in the lighted culture cabinet could be attributed mostly to the metabolism of the bacteria and phytoplankton. At least it can be stated that within 24 to 48 hours after the $P^{32}$ was added, up to 98 percent of it had been removed from the water by particles large enough to be retained on a millipore filter disc. This disc will retain particles with a diameter of at least 0.5 micron.




IGURE 3.—Effect of numbers of *Nitzschia closterium* cells on their rate of removal by the hard clam.

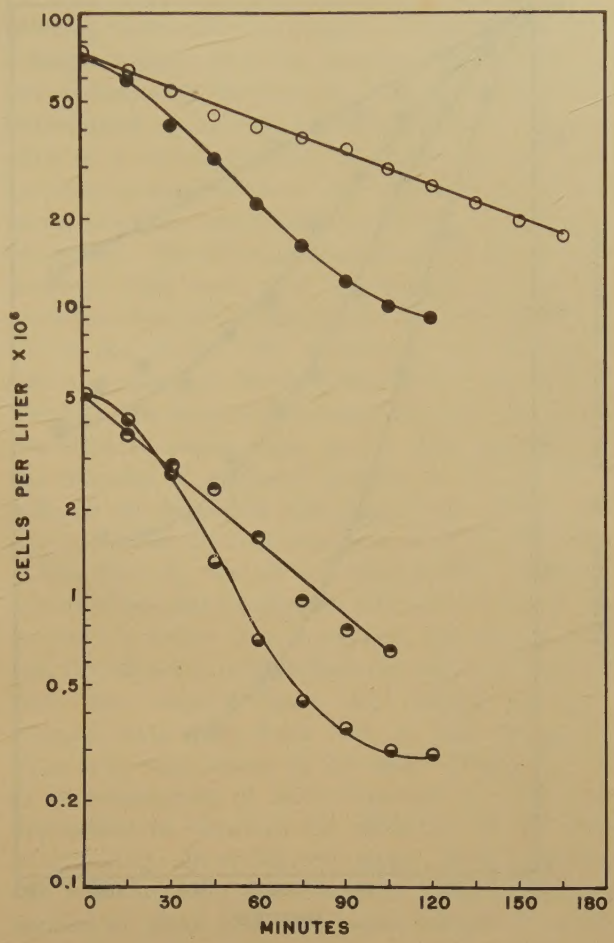



FIGURE 4.—Comparison of rates of removal of a species of phytoplankton by clams in unialgal and in mixed algal suspension. (○ = *Nannochloris* cells in unialgal suspension; ● = *Nannochloris* cells mixed with *Nitzschia closterium* cells; ◓ = *Nitzschia closterium* cells mixed with *Chlorella* cells; and ◒ = *Nitzschia closterium* cells in unialgal suspension.)

This heterogeneous assortment of particles, including bacteria, planktonic algae, and inanimate particles, was removed from the water by clams at a faster rate than *Nannochloris* cells were filtered, but not quite as rapidly as *Nitzschia closterium* cells (fig. 5). This may be representative of the rate of removal of particles under natural conditions, since a microscopic examination of a portion of the fresh sea water revealed the presence of green algae as well as diatoms. Thus, one would expect the rate of removal of the natural population to fall between the filtering rates found for green algae and for diatoms in unialgal suspensions.

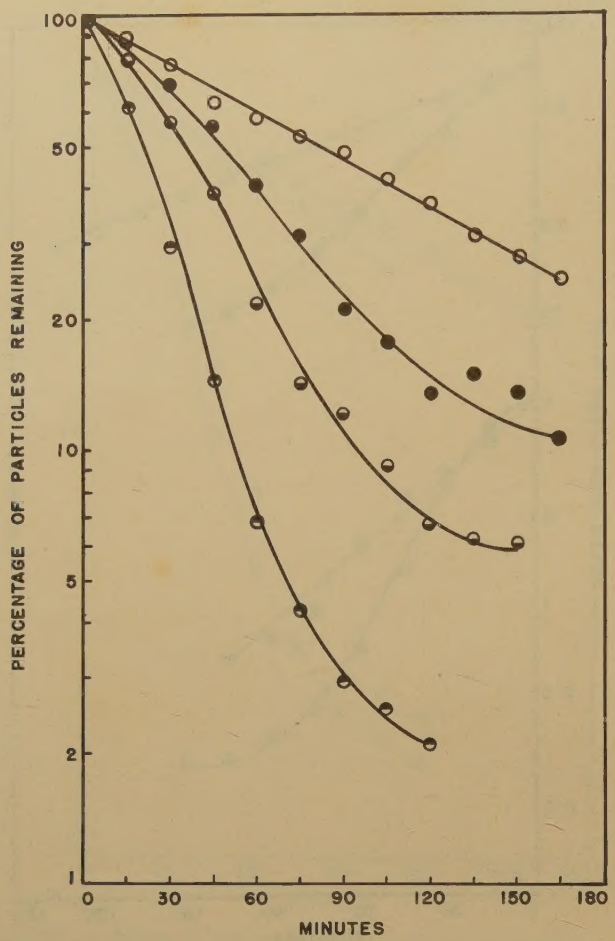



FIGURE 5.—Comparison of rates of removal of particles from freshly collected sea water with that of *Nannochloris* cells and of *Nitzschia closterium* cells. (○ = *Nannochloris*; ● and ◒ = Particles from freshly collected sea water; and ◓ = *Nitzschia closterium*.)

The clam, a bottom-burrowing animal, may frequently be confronted with the problem of filtering cells from water that is heavily laden with silt. The silt used in these experiments was collected from an intertidal area. Care was taken to obtain silt that was as free from sand as possible. After several washings in sea water the silt was washed through cheese cloth and allowed to settle. The water was decanted from the silt, which was spread out and dried. The silt was then pulverized and stored in a glass-stoppered bottle until used.

Two approaches were used to determine the effect of silt on the rate of removal of *Nitzschia closterium* cells from the water. The first method was to add dried silt to the water in which the clam was to be placed just before the experiment. The silt would settle out of the water in a few minutes, even though the water was being vigorously stirred. A second method was to add the same amount of dried silt to sea water several days before the feeding experiment was carried out. When prepared in this manner, the silt remained in suspension a greater length of time than when added just before the experiment. The effect of 10 grams of dried silt per 2 liters of water on the rate of removal of *Nitzschia closterium* cells is shown in figure 6. For a short time following addition of the dry silt the rate of removal of cells by the clam was not as rapid as before or after this time. The addition of silt that had been placed in water several days before the experiment caused the same response in the clams but to a greater extent. A large amount of mucus was formed by the clam, apparently in an effort to remove the silt from the water. This silt-laden mucus often formed an uneven border around the edge of the shell, in addition to its floating in clumps in the water. In not one of the experiments did a clam close when silt was added to the water. We probably can assume that fewer cells were ingested by the clam during the time silt was present, since so much mucus was released in the water.

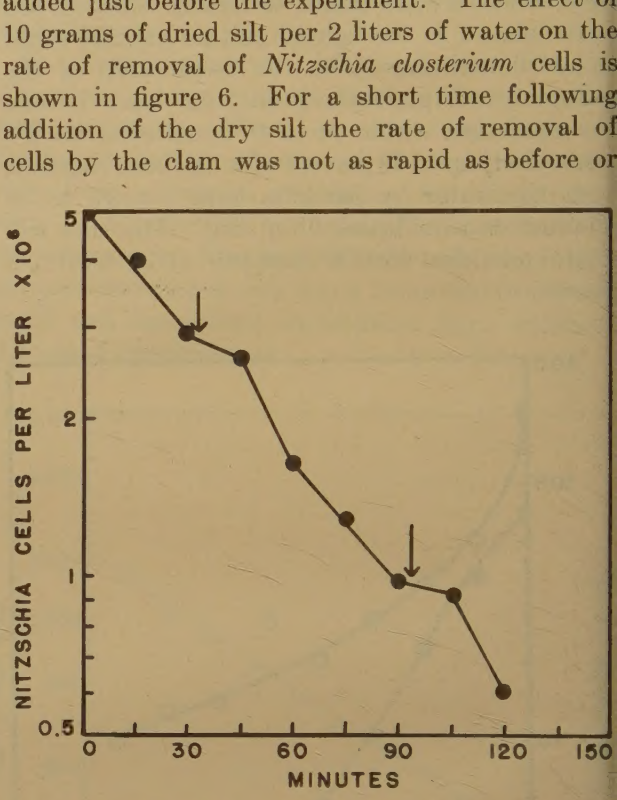



FIGURE 6.—Rate of removal of *Nitzschia closterium* cells by the clam showing effect of an addition of 10 grams of dried silt. (Arrows indicate time silt was added.)

## DISCUSSION

Since radioactive-labeled phytoplankton was sed in these investigations, we could follow its ate of removal under various conditions. Low opulation sizes, such as 400,000 *Nitzschia* cells er liter used in one series of experiments, could ot have been accurately measured initially, and specially throughout the experiment as the num-er of cells decreased, if the measurements had ot been based on radioactivity. Since the amount f radioactive phosphorus per cell can be varied ver a wide range, it is possible to prepare sus-ensions of cells with large or small populations o that a sample, regardless of the number of cells resent, will give an accurate radioactivity meas-rement. In addition, labeled cells from small ortions of suspension taken at frequent intervals ill give accurate measurements. In the silt ex-eriment, the rate of removal of the *Nitzschia* cells ould not have been followed with photometric ethods due to interference from the silt. Neither ould photometric methods have been used to easure a reduction in the number of cells of one ecies of algae when another species was also resent, as in mixed suspensions. Finally, the mparison made between rates of removal in atural populations and in unialgal cultures was ossible when it was based on the removal of adioactive-labeled particles. These are among he many advantages associated with the use of adioisotopes in investigations similar to those resented here.

Filtering rates obtained with hard clams in uni-lgal suspensions of planktonic algae varied con-derably with the species used. In suspensions f small cells of either *Nannochloris* or *Chlorella*, he highest filtering rate seldom exceeded 2 liters er hour, but in suspensions of diatom cells the ighest average filtering rate exceeded 5 liters per our. This difference could have been due to a reater efficiency in the retention of the diatoms y the filtering mechanism of the clam or to an ncreased rate of pumping water through the filter-ng mechanism in the presence of the diatoms. In ne with present-day thinking, the clam appar-ntly filters more water in suspensions of the larger ells because of a more efficient retention of the ells from the water pumped by the clam. How-ver, if the clam does remove the smaller, algal ells as efficiently as the diatoms, then the higher filtering rates with the diatoms would reflect only a larger volume of water pumped by the clam in the presence of the diatoms. As far as could be determined, an increased pumping rate in the presence of a certain species of algae has not been reported in the literature, but this does not necessarily eliminate the possibility of such an increase occurring. The filtering rates obtained when *Nannochloris* cells were used in unialgal suspensions were less than when *Nitzschia* cells were also present in the water. The reason for this increased rate of removal of *Nannochloris* cells is not known. Possibly, the presence of *Nitzschia* cells stimulated the clam to pump more water, thus resulting in the removal of a greater number of *Nannochloris* cells, or the *Nitzschia* cells clogged the gills resulting in a more efficient retention of *Nannochloris*.

The filtering rate of the clam based on the removal of planktonic algae is a function of both the amount of water that is pumped per unit of time and the efficiency with which the cells are removed from this water. Since the volume of water pumped may vary from time to time when the clam is in suspensions of the same species, as well as in suspensions of more than one species, it is impossible to compare the efficiency of the clam in removing cells of different sizes. With a method for following the simultaneous removal of two species of algae from the same volume of water being pumped and filtered by the clam, the relative efficiency of removal of the cells could be measured. Even though the volume of water pumped could not be calculated any more accurately, it would be one and the same volume and could be eliminated as a factor influencing the amount of water filtered. Any differences in the filtering rates obtained by calculations from the rates of removal of two species from the same volume of water would be a reflection of the difference in the efficiency of the clam in removing the two species of algae. The simultaneous removal of two species of algae from the same volume of water can be followed with radioisotopes. This is possible, since one species of algae can be labeled with one isotope while the other species is labeled with a second isotope. Then, with radiological techniques, measurements can be obtained from which calculations can be made showing the number of cells of each species removed in a given period of time. Experiments using this approach are now being conducted in our laboratory.

It was found that the amount of water filtered per gram of meat by clams in suspensions of *Nannochloris* decreased as the weight of meats increased. Similar results were also observed for the bay scallop (Chipman and Hopkins, 1954). Whether this difference in volume of water filtered by the clam was due to a higher metabolic rate in the smaller clam or was the result of less gill surface per gram of meat in the larger clam was not investigated. The filtering rate for the adult clam, whether based on the removal of small algal cells or of diatoms, is much less than that observed for the bay scallop and the oyster. The adult bay scallop was found to filter an average of 14 liters of water per hour (Chipman and Hopkins, 1954). The oyster from New England waters has been reported to pump from 6 to 15 liters per hour (Nelson, 1935, 1936; Loosanoff and Nomejko, 1946; Loosanoff and Engle, 1947; and Loosanoff 1950).

The filtering rate of filter-feeding animals does not necessarily indicate the feeding rate, since all food particles removed from the water do not have to be ingested. According to MacGinitie (1941) feeding occurs only when a mucous sheet is present. The importance of mucus for the ingestion of food has been discussed by Jørgensen (1949) and Jørgensen and Goldberg (1953). It is believed by Ballantine and Morton (1956) that the greatest stimulus to mucous secretion is the presence of large amounts of indigestible debris in the water. In the present investigation, no observations on the formation of mucus in relation to the ingestion of food were made, but the rejection of food under certain conditions as indicated by the occurrence of pseudofeces in the water was closely followed. It can be stated that the number of cells present in the water, the presence of nonliving particles such as silt, and the particular plankton species with its associated physical and chemical characteristics influence the amount of food which will be rejected as pseudofeces.

That the number of cells present in the water could influence the feeding of lamellibranchs was suspected by Kellogg as long ago as 1915 (Kellogg 1915). Later Loosanoff and Engle (1947) showed experimentally that there are definite concentrations above which the numbers of food organisms begin to interfere with the feeding of oysters. In experiments in this investigation in which large numbers of *Nitzschia* cells were used, large amounts of pseudofeces were released to the water. When only small or intermediate populations of *Nitzschia closterium*, as well as the cells of other species, were present in the water, pseudofeces were not observed. When clams were in water containing large amounts of algal cells the formation of pseudofeces probably was due to the mechanical overloading of the gills and palps with a greater quantity of cells than could be ingested.

The influence of silt, along with several other substances, upon the rate of feeding of the oyster has been investigated by Loosanoff and Tommers (1948). They observed about a 94-percent decrease in the average rate of pumping when 3 to 4 grams of silt per liter of water were added. In our clam experiments, there was an instant and marked reduction in the filtering rate upon addition of 5 grams of silt per liter of water; however this effect lasted for only a brief time. After about 15 minutes the clam was filtering *Nitzschia* cells from the water at a rate faster than that before the silt was added. Within 30 minutes after the silt was added, the clam was again filtering *Nitzschia* cells from the water at a normal rate. It was observed that not one clam closed during our experiments in which silt was added to the water. Loosanoff and Tommers (1948) in their experiments also found that a majority of the oysters kept their shells open most of the time when silt was added.

From our experiments it appears that the *Chlorella* cells had an unfavorable effect upon the filtering rate of the clam. It was observed that clams, which in previous experiments with other species of algal cells had remained open consistently during the entire period of sampling, usually opened and closed at irregular intervals in the presence of *Chlorella*. Also these clams were the only ones that remained closed for some time when returned to running sea water. Since filtering rates used in this investigation were based on continuous sampling for periods of up to 3 hours, the irregular opening and closing of the clam in the presence of *Chlorella* made it difficult to obtain data for that species. Even though *Chlorella* cells are somewhat larger than *Nannochloris* cells, the filtering rate was usually lower for clams in suspensions of *Chlorella*. Almost always large quantities of pseudofeces were formed when the clam was in suspensions of *Chlorella*. This occurred in suspensions of other

ecies of algae only when large numbers of cells ere present. The presence of *Chlorella* cells in ixed suspensions with another species resulted a lowered filtering rate for the other species. om our experiments it is also apparent that the der *Chlorella* cultures had a more pronounced fect than the newer cultures.

## SUMMARY

The filtering rate of the hard clam, *Venus ercenaria* L., was determined in a series of periments in which the clams were placed in ialgal and mixed suspensions of radioactive-beled phytoplankton. The term "filtering rate" as interpreted to mean the volume of water from hich the phytoplankton or other particles were moved per unit of time. Four species of uni-llular algae were used in these experiments.

1. A comparison of filtering rates of the same am in various concentrations of *Nannochloris* iring a period of 2½ months showed no correlation tween initial concentration of this algal species d its rate of removal.

2. More water was filtered per gram of meat small clams than by large ones.

3. Clams had higher filtering rates in suspen-ons of diatoms than in suspensions of the smaller een algae. In suspensions of diatoms, the erage filtering rates ranged from 3 to 6 liters r hour, while in suspensions of green algae the ghest average filtering rates rarely exceeded liters per hour.

4. Filtering rates were less in suspensions of atoms containing either small numbers (400,000 r liter) or large numbers (170 million per liter) an in suspensions containing intermediate num-rs (5 million to 75 million per liter).

5. When diatoms were in mixed suspensions th *Nannochloris* the average filtering rates, based the rate of removal of *Nannochloris*, were higher an those obtained when the clam was in unialgal spensions of *Nannochloris*. Lower average filter-g rates were obtained for the clam in mixed spensions of *Nitzschia closterium* and *Chlorella* lls than in unialgal suspensions of *Nitzschia*.

6. The filtering rate of the clam was higher in tural phytoplankton populations than in uni-gal suspensions of green algae, but lower than in ialgal suspensions of diatoms.

7. Addition of silt to algal suspensions resulted in an instantaneous decrease in the filtering rate of the clam.

8. The clam formed large quantities of pseudo-feces in the presence of high concentrations of algae, in all suspensions of *Chlorella*, and after silt was added.

## LITERATURE CITED

Ballantine, Dorothy, and J. E. Morton.
1956. Filtering, feeding, and digestion in the lamelli-branch, *Lasaea rubra*. Jour. Marine Biological Association United Kingdom 35 (1): 241–274. London.

Chipman, Walter A., and Jean G. Hopkins.
1954. Water filtration by the bay scallop, *Pecten irradians*, as observed with the use of radioactive plankton. Biological Bull. 107 (1): 80–91.

Cole, H. A., and B. T. Hepper.
1954. The use of neutral red solution for the comparative study of filtration rates of lamellibranchs. Jour. du Conseil 20 (2): 197–203.

Collier, Albert, S. M. Ray, A. W. Magnitzky, and Joe O. Bell.
1953. Effect of dissolved organic substances on oysters. U. S. Fish and Wildlife Service, Fishery Bull. 54 (84): 167–185.

Fox, Denis L., H. U. Sverdrup, and John P. Cunningham.
1937. The rate of water propulsion by the California mussel. Biological Bull. 72 (3): 417–438.

Galtsoff, Paul. S.
1926. New methods to measure the rate of flow produced by the gills of oyster and other molluscs. Science (n. s.) 63: 233–234.
1928. Experimental study of the function of the oyster gills and its bearing on the problems of oyster culture and sanitary control of the oyster industry. U. S. Bureau of Fisheries, Bull. 44 (Doc. No. 1035): 1–39.

Jørgensen, C. C. Barker.
1943. On the water transport through the gills of bivalves. Acta Physiologica Scandinavica 5: 297–304.
1949. The rate of feeding by *Mytilus* in different kinds of suspension. Jour. Marine Biological Assoc. United Kingdom 28 (2): 333–344. London.

Jørgensen, C. C. Barker, and Edward D. Goldberg.
1953. Particle filtration in some ascidians and lamellibranchs. Biological Bull. 105 (3): 477–489.

Kellogg, James. L.
1915. Ciliary mechanisms of lamellibranchs, with description of anatomy. Jour. Morphology 26 (4): 625–701.

Loosanoff, Victor L.
1950. Rate of water pumping and shell movements of oysters in relation to temperature. Anatomical Record 108 (3): 620. Wistar Institute Anatomy and Biology, Philadelphia. [Abstract.]

LOOSANOFF, VICTOR L., and CHARLES A. NOMEJKO.
1946. Feeding of oysters in relation to tidal stages and to periods of light and darkness. Biological Bull. 90 (3): 244–264.

LOOSANOFF, VICTOR L., and FRANCIS D. TOMMERS.
1948. Effect of suspended silt and other substances on rate of feeding of oysters. Science (n. s.) 107: 69–70.

LOOSANOFF, VICTOR L., and JAMES B. ENGLE.
1947. Effect of different concentrations of microorganisms on the feeding of oysters (*O. virginica*). U. S. Fish and Wildlife Service, Fishery Bull. 51 (42): 31–57.

MACGINITIE, G. E.
1941. On the method of feeding of four polecypods. Biological Bull. 80 (1): 18–25.

NELSON, THURLOW C.
1935. Water filtration by the oyster and a new hormone effect thereon. Anatomical Record 64 (1): 68. Wistar Institute Anatomy and Biology, Philadelphia. [Abstract.]
1936. Water filtration by the oyster and a new hormone effect upon the rate of flow. Proceed. Soc. Experimental Biology and Medicine 34: 189–190. New York.

RAO, K. PAMPAPATHI.
1953. Rate of water propulsion in *Mytilus californianus* as a function of latitude. Biological Bull. 104 (2): 171–181.

RICE, THEODORE R.
1953. Phosphorus exchange in marine phytoplankton. U. S. Fish and Wildlife Service, Fishery Bull. 54 (80): 77–89.

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